UNIVERSITY OF ALBERTA

SIMULATED FIRE SEVERITY AND SEEDLING GROWTH AT TREELINE: A CLIMATE CHANGE ANALOGUE

BY

Sue K. Olsen, B.Sc.F

(C)

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Simulated fire severity and seedling growth at treeline: a climate change analogue** submitted by **Sue K. Olsen** in partial fulfillment of the requirements for the degree of **Master of Science**.

R.W. Wein

G.P. Kershaw

S.E. MacDonald

April 16, 1993

to my wee mum -
on the other side of Canada in body,
but in spirit -
right beside me with a cuppa tea and a cheery smile

ABSTRACT

The response of vegetation to a change in climate is predicted to occur first at ecotones, where species are growing at the limit of their range. Fire severity, post-fire moisture and temperature conditions were experimentally manipulated on 54 plots 1.5x1.5m in size at treeline near Inuvik, NT. Replicated (n=3) treatments of fire severity (lightly, moderately, heavily burned), moisture (-50%, normal, +50%) and temperature (ambient, +1 to 4°C) were randomly assigned to these plots. Each treatment plot was sown with black spruce, paper birch and balsam poplar seeds during summer 1991. Container black spruce, paper birch and baslam poplar seedlings were planted in the plots during summer 1992.

First-year percent emergence for all species increased as the simulated level of fire severity increased from lightly to heavily burned. In addition, paper birch emergence on the higher temperature plots was almost twice that on the ambient temperature plots. For all species, first-year seedling shoot growth was not significantly different among treatments. An increase in fire severity significantly increased black spruce winter survival. Birch seedling leaf area also increased as fire severity increased. Second-year poplar shoot growth was affected by the interaction of the three treatments with the greatest growth measured on the lightly burned treatments with high temperature and high moisture conditions.

At treeline, fire may be a vital agent in replacing less-suited species with those more adapted to the climate-modified conditions.

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INTRODUCTION

Under the driving force of an enhanced greenhouse climate, General Circulation Models (GCM's) consistently predict a greater degree of warming in the northern hemisphere as latitude increases (Bolin *et al.* 1986, Roots 1989, Bonan *et al.* 1990). Winter warming at the poles is predicted to be 3 to 4 times that of summer warming (Maxwell and Barrie 1991). Warmer winter temperatures may translate into an earlier spring and delayed onset of autumn, thus a longer growing season. Potentially, surface and fine fuels will dry earlier in the spring, and surface and subsurface fuels may stay dry longer into the fall. This may result in a longer fire season in northern Canada (Flannigan and Van Wagner 1991). The ability of GCM's to predict precipitation is limited and there is uncertainty regarding the frequency of drought with greenhouse warming. Mitchell and Warrilow (1987) suggest greater increases in winter and spring precipitation at high latitudes, but more summer drought.

It has been suggested that the interaction between higher temperatures on the surface of earth and the predicted cooler tropopause will cause more pronounced climatic variability in the future (Rind et al. 1989). Rind *et al.* (1989) suggest that exceptional weather conditions may become more common in Canada over the next several decades. On a biome basis, the response of vegetation to a change in climate is predicted to occur first at ecotones (Elliott-Fisk 1983, Cwynar and Spear 1991, Rizzo and Wiken 1992), where species are growing at the limit of their range.

Fire is considered to be the most important stochastic event causing vegetation change in the northern boreal forest (Wein and MacLean 1983). Under changing climatic conditions, fire may be a vital agent in replacing less-suited species with those more adapted to the modified climate (Brubaker 1986, Overpeck et al. 1990). In Alaska, Viereck (1979) predicted that tree distribution may expand if tundra fires near treeline provide favourable seedbeds for seedling germination and establishment.

The fire which burned in the forest-tundra close to Inuvik in 1968 is a good example of how exceptional weather conditions, in this case a prolonged period of warm, dry weather in early August, can affect fire behaviour. This fire was exceptionally severe and burned through much of the thick surface organic layer to expose mineral soil over most of the 500 km^2 burn area (Wein 1975). Severe fires, like this one, dramatically change the pre-fire organic soil dominated system to a mineral based system and can influence the post-fire successional sequence (Viereck and Schandelmeier 1980). Twenty two years after the Inuvik fire,

Landhaeusser and Wein (1993) found poor recovery of black and white spruce in previously treed areas. Post-fire densities of paper birch and balsam poplar had increased and both of these species had extended their range into previously untreed areas.

Prentice (1986) has suggested that successional response times depend to a large extent on the life history characteristics of the species involved in succession. Fire plays a vital role in the reproduction and regeneration of six northern tree species (black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), paper birch (*Betula papyrifera* Marsh.), balsam poplar (*Populus balsamifera* L.), trembling aspen (*P. tremuloides* Michx.) and tamarack (*Larix laricina* (Du Roi) K. Koch)) by removing competing vegetation, exposing seedbeds, opening semi-serotinous cones of black spruce and altering the thermal regime of the soil for seedling establishment (Viereck and Schandelmeier 1980).

Black spruce can reproduce both sexually and vegetatively by layering. Although black spruce is usually killed by fire, the seed supply is rarely consumed. Black spruce seed matures in late summer and in the absence of fire a portion of the seed is dispersed throughout the year, although most of the seed remains in the cones. Viable seeds can remain in the cone for at least 20 years after fire (Wein 1975). Black spruce seeds germinate well on exposed mineral soil (Viereck and Johnston 1991).

Paper birch dominates early in the successional sequence (Viereck and Schandelmeier 1980), declining only when soil temperatures decrease due to organic buildup (Van Cleve *et al.* 1982). Paper birch is readily killed by fire. However, it quickly re-invades exposed mineral soil by seeding from outside the burned area and by vegetatively reproducing from basal buds (Safford *et al.* 1991). Birch produces an abundant supply of small winged seeds which ripen in late summer and are dispersed through the winter until the following summer. In the boreal forest, Zasada *et al.* (1991) found paper birch seeds to be viable for up to six years after dispersal. Moderate dispersal distances are attained in windy weather over the snowpack.

Balsam poplar and trembling aspen reproduce vegetatively from basal and root buds, as well as by lightweight, wind dispersed seed. The seeds are short-lived and there is no evidence that they overwinter and germinate the following spring (Zasada *et al.* 1991). Like paper birch, poplar and aspen establishes early in the successional sequence (Zasada *et al.* 1991).

A severe fire, in conjunction with future climate change predictions, may displace, eliminate or expand the current abundance and range of tree species growing near treeline (Landhäusser and Wein 1993). Landhäusser and Wein (1993) hypothesize that the disturbance of fire as a result

of changed climatic parameters may provide the blend of environmental conditions required for tree species to expand northward in the decades following fire.

The objective of this study was to experimentally determine the effects of simulated fire severity and post-fire temperature and moisture conditions on the emergence, winter survival and shoot growth of black spruce, paper birch and balsam poplar near Inuvik, NT.

STUDY AREA AND METHODS

General study area

The general study area was located in the uplands within the southern portion of the Mackenzie Delta, near Inuvik, Northwest Territories at approximately 68°21' north Latitude and 133°43' west Longitude.

The delta is post-glacial in age and most of the sediments were deposited during the last 5000 years (Mackay 1978). The soils are generally poorly developed due to continuous permafrost and cryoturbation processes (Day and Rice 1964). In areas with a deep seasonal active layer (more than 50cm), soils range from Regosolic Static Cryosols on the dry sites through Orthic to Brunisolic Static Cryosols on the moist sites. The mineral soils are composed of fine textured clays to silty clay loams and are usually overlain by 20 to 30cm of surface organic matter (Day and Rice 1964).

Continuous permafrost underlies most of the Mackenzie Delta region (Mackay 1978). Topography in the southern part of the delta is characterized by flat morainal plains.

The climate near Inuvik is classified as High Subarctic (Ecoregions Working Group 1989) (Figure 1). Based on the 30-year record (1951-1981), the snow-free period is short and cool, generally lasting about four months. The growing season is much shorter: about two months. The average July temperature is 13.3°C, although mean daily temperatures have gone from as high as 31°C to below freezing. Frosts are common throughout the summer. Winters are long and cold. The mean January temperature is -29.4°C. Mean total annual precipitation ranges from 250 to 350mm, with most falling in the late summer and early fall. Snowmelt typically occurs during the third week in May, and the first permanent snowfall occurs after the first week in September (Burns 1973).

The Inuvik area is near the northernmost extension of the boreal forest region (Rowe 1972). The vegetation in this area is transitional between forest and tundra. The forest component is dominated by black spruce. Paper birch and white spruce dominate the warm, southern exposures, while black spruce and tamarack commonly grow in the low-lying areas. Balsam poplar and aspen grow along the river valleys. The understory vegetation is predominantly alder (*Alnus crispa*), dwarf birch (*Betula glandulosa*), willow (*Salix spp.*), Labrador tea (*Ledum groenlandicum, Ledum palustre*), and other heath species such as cranberry (*Vaccinium vitis-idaea*), crowberry (*Empetrum nigrum*), cloudberry (*Rubus chamaemorus*) and many species of lichens and mosses.

Site desciption

In June of 1991, three study sites were located within the forest near Inuvik, NT (Figure 2). The vegetation at each site can generally be described as a "drunken forest" (Pettapiece 1974) and is representative of the forest-tundra region in the western Canadian Arctic. Cryoturbation, causing earth hummocks, has tilted many of the trees. The overstory vegetation was predominantly black spruce standing approximately three to seven metres high; the age of each stand was 150 to 200 years. The dominant members of the shrub understory were: alder, willow, dwarf birch, Labrador tea and bog cranberry. The ground layer consisited of some lichen patches (i.e. *Cladonia* spp.), peat mosses (*Sphagnum spp.*), brown mosses (i.e. *Tomenthypnum nitens*) and feather mosses (*Pleurozium shreberi*).

Silty clay mineral soil was overlain by approximately 20 to 30cm of organic soil. Site aspect was south-east to south-west and slope was, on average, about 2-3%.

Experimental design

Fixed factors within each site were the simulated treatments of fire severity (three levels), moisture (three levels) and temperature (two levels). Random factors were the seeds, seedlings and blocks.

Within each site, 18 plots were laid out and one of 18 treatments was randomly assigned to each plot. Each treatment plot measured 1.5 x 1.5m and each site measured approximately 50 x 50m. Plots within each site had similar slope, vegetation composition and depth of organic soil. Three levels of fire severity (heavy, moderate and light) were simulated by the manual removal of organic material. Following Weber (1975), Viereck *et al.* (1979) and Woodley (1979), severity treatments were characterized by the amount of organic matter removed from the plot. For the "light burn" plots, only the surface vascular vegetation and leaf litter was removed. For the "moderate burn" plots, the surface vascular vegetation and leaf litter was removed, in addition to approximately half of the organic soil. And for the "heavy burn" plots, the surface vascular vegetation, litter and all of the organic soil was removed.

One of three moisture treatments (average monthly rainfall, +50%, -50%) and one of two temperature treatments (ambient, ambient + approximately 3°C) were randomly allocated to each plot at the same time as the fire severity treatments were allocated. In order to control temperature and moisture conditions, a sloping plastic sheet was mounted on a wooden frame and placed over each plot. This sheet protected the plots from rainfall. For the ambient air temperature treatment the plastic sheet was positioned

approximately 1m above the soil surface. Higher temperatures were simulated by positioning the plastic sheet closer to the ground (approximately 60cm above the soil surface) and by fastening plastic sheets on three sides of the plot in order to slow air movement.

The moisture treatments were based on the average monthly precipitation records for Inuvik (1951-1981).

Methods

Air and soil temperature

In order to characterize air and soil temperatures over a growing season, 20 gauge copper-constantan thermocouples were installed in each plot at site 1. Shielded air temperature (at 20cm) and soil temperatures at 0cm (germination zone), 5cm depth (initial rooting zone) and 15cm depth (second year rooting zone) were measured approximately twice weekly throughout the growing season of 1992. All temperature measurements were taken between 1400 and 1600 hours (the sun reached its maximum height at 1500 hours). In order to estimate the difference in degree-hours between the three levels of fire severity treatments, soil and air temperature was also measured at site 1 at regular intervals on 5 August 1992.

Active layer depth

The active layer was measured on all treatment plots at all sites using a 1cm stainless steel probe. In mid-August, twelve measurements were taken in the centre (60 x 60cm) of each plot.

Seedling emergence, shoot growth and winter survival after direct seeding

Black spruce seed was collected from several trees in Inuvik during August 1990. Following Safford (1974), the cones were air-dried, and the seeds were extracted by vigorous shaking. Black spruce seed germinability was 95%.

At the same time, the mature strobiles of paper birch were picked from trees, air-dried and then the seed was mechanically separated (Brinkman 1974). Paper birch seed germinability was 85%.

The spruce and birch seed was refrigerated in sealed containers at 2°C, then stratified at 4°C for two weeks in early June 1991 using filter paper moistened with a 1% solution of the fungicide Thiram.

Balsam poplar catkins were collected along the east channel of the Mackenzie River near Inuvik, NT in mid-July 1991. Seeds were separated with a strong air-stream. Balsam poplar seed germinability was 99%.

In mid-July 1991, two hundred seeds of paper birch and one hundred seeds each of black spruce and balsam poplar

were sown in each plot. To simulate natural seedfall and germination conditions, the black spruce and birch seeds were buried under approximately 1cm of organic material/litter and the poplar seed was sown directly on the surface soil. The plots were watered at a rate of 2.2 mm per plot for the first three days following sowing. After this time, the regular watering schedule was followed (Table 1).

Emerging seedlings were monitored weekly until mid-August 1991. To avoid competition effects, recolonizing plants were regularly clipped from each plot throughout the summer. In mid-August, all except ten seedlings of each species in each plot were collected for shoot measurements. Shoot length of the remaining seedlings was measured in the field. The remaining ten seedlings were used to estimate the percentage of successfully overwintering seedlings. To determine the success of overwintered seedlings, the number of live seedlings were counted in early June 1992.

Due to flooded conditions, 14 of the heavily burned treatment plots were relocated in spring 1992.

Shoot growth and leaf area of planted seedlings

Black spruce, paper birch and balsam poplar seed was collected in July and August of 1991 in the same way as described for 1990. The seed was then transported to the laboratory and refrigerated in sealed containers at 2°C. In late December 1991, the seeds were transferred to a growth chamber where they were sown in petri dishes moistened with a 1% solution of Thiram. During germination, photoperiod in the growth chamber was 24 hours and the temperature was 25°C. Approximately 450 germinants of each species were transplanted into 20cm^3 Spencer Lemair seedling containers with a 60/40 peat:sand mixture. Photoperiod was reduced to 18 hours; day temperature remained at 25°C, but night temperature was lowered to 20°C. After the third week, the seedlings were fertilized once a week with a 20-20-20 nitrogen-phosphorus-potassium fertilizer solution. To facilitate transport to Inuvik, NT., the seedlings were hardened off in mid-March 1992. Daylength in the growth chamber was reduced by three hours weekly and the temperature was reduced by 3°C weekly to a minimum day temperature of 10°C and a minimum night temperature of 6°C. Watering was reduced to once a week and the seedlings were no longer fertilized. All seedlings were then air cooled in the dark for one month at 2°C and balsam poplar was stored at -5°C for an additional week.

In mid-June, 1992, all plots established in 1991 were cleared of vegetation and three black spruce, four paper birch and four balsam poplar seedlings were planted in separate rows in each plot. The height of each seedling was measured at this time. At the end of the growing season

(mid-August), the seedlings were collected and shoot growth was measured on each seedling. Leaves were removed from each paper birch and balsam poplar seedling and leaf area was measured manually.

Statistical analysis

A three-way Analysis of Variance model (Appendix 1) tested for the treatment effects of fire severity, temperature and moisture on first-year emergence, shoot growth, winter survival and second-year shoot growth of black spruce, balsam poplar and paper birch. Treatment effects on second-year leaf area for paper birch and balsam poplar were also calculated.

RESULTS

Air and soil temperature

Air temperature on the high temperature treatment plots averaged between 1-4°C higher than the ambient temperature treatments, but decreased with increasing soil depth (Table 2). For the lightly and moderately burned treatments, soil temperature was similar at all depths. Temperatures on the heavily burned treatments were lower than those on the lightly and moderately burned treatments. There was little temperature difference among the three levels of fire severity at the 15cm soil depth.

On August 5, 1992, the degree hours (effective temperature sum) at a depth of 5cm, using a base of 5°C, were highest for the lightly burned treatment (48), slightly less for the moderately burned treatment (45) and lowest for the heavily burned treatment (29) on 5 August 1992.

Active layer depth

Fire severity significantly influenced ($p<0.0001$) the depth of the active layer (Appendix 2). Active layers on the lightly and moderately burned treatments were much thinner (43cm for both) than those of the heavily burned treatments (55cm) (Table 3). It could not be demonstrated that moisture or temperature treatments significantly affected active depths (Appendix 2; $p=0.105$, $p=0.987$, respectively).

First-year growth

Seed emergence

As the simulated level of fire severity increased from light to heavy, percent seedling emergence increased for all species ($p<0.0001$ for all species) (Figure 3; Appendix 3). After adjustment for viability, black spruce and balsam poplar showed the highest percentage emergence from the mineral soil of the heavily burned treatment (36% and 38%, respectively), while only 16% of the paper birch seeds emerged on the heavily burned treatment. Emergence of black spruce, paper birch and balsam poplar seedlings was very low on the lightly and moderately burned treatments. Moisture and temperature treatments showed no significant effect on seed emergence of any of the species (Appendix 3).

Paper birch emergence on the heavy burn treatment was influenced by temperature treatments ($p=0.054$, Appendix 3). Seed emergence on the high temperature-heavy burn plots was almost twice that of the ambient temperature-heavy burn plots (Figure 4).

Shoot growth

The treatments of fire severity, moisture or temperature did not significantly affect first-year growth of black spruce, paper birch or balsam poplar (Appendix 4).

Winter survival

Fire severity significantly affected the winter survival success of black spruce seedlings ($p=0.031$), but had no demonstrated effect on the survival of paper birch or balsam poplar seedlings (Appendix 5). As fire severity decreased, the percentage of surviving spruce seedlings increased from 22 ± 4 to 78 ± 12. The temperature and moisture treatments did not significantly influence winter survival of any of the three species.

It appeared that processes associated with needle ice formation killed many of the overwintering seedlings.

Second year growth of planted seedlings

Shoot growth

It could not be demonstrated that fire severity, moisture or temperature treatments significantly affected second-year shoot growth of the planted black spruce or paper birch seedlings (Appendix 6). Poplar seedling growth on the lightly burned treatments responded to the temperature treatment differently at different levels of moisture ($p=0.021$) (Table 4; Appendix 6).

Poplar seedling growth was greatest on the lightly burned, high temperature, high moisture treatment. The least amount of growth occurred on lightly burned, normal precipitation, ambient temperature treatments.

Leaf area

The leaf area of paper birch increased with increasing fire severity treatments ($p=0.028$). Average birch leaf area (with standard errors) for lightly burned, moderately burned and heavily burned treatments were $83cm^2\pm8$, $102cm^2\pm7$ and $112cm^2\pm6$, respectively. Fire severity, moisture and temperature treatments did not significantly affect the leaf area of balsam poplar seedlings (Appendix 7).

DISCUSSION

The effect of fire on site conditions is a function of the fire regime, including fire severity (Wein and MacLean 1983). A severe fire in northern ecosystems removes organic surface soil horizons, leaving mineral soil horizons exposed. Seed germination and early seedling growth on mineral soil has been shown to be much better than on organic soils (see Wein 1975, Dyrness and Norum 1983, Zasada *et al.* 1983, 1987, 1991, Sirois and Payette 1989).

Moisture and temperature have been cited as the most critical factors for seedling germination (Black and Bliss 1980, Foster 1985, Sirois and Payette 1989, Zasada *et al.* 1991), especially on organic seedbeds (Thomas and Wein 1985, Zasada *et al.* 1991). The significant increase in seedling emergence for all three species as fire severity increased was likely related to the low water retention capacity of the less severely burned organic surfaces (Sirois and Payette 1989).

Tryon and Chapin (1983) reported that species not adapted to cold temperatures are often the most temperature sensitive. Paper birch, the only species in my experiment responding to different levels of temperature, generally grows on warm, well drained south-facing exposures. Black spruce and balsam poplar commonly grow in cooler, more moist areas where they may be exposed to colder temperatures (see Viereck and Foote 1970, Van Cleve *et al.* 1983, Viereck *et al.* 1983). The ambient temperature treatment in this experiment may have been relatively less favourable for paper birch seed emergence, than for black spruce or balsam poplar emergence.

Zasada *et al.* (1987) found that fire severity positively influenced early shoot growth of several trees and shrubs growing in Alaska. In my experiment, poplar second-year shoot growth was significantly affected by the interaction of simulated fire severity, moisture and temperature. On the lightly burned treatments, shoot growth on the normal and high moisture treatments increased as temperature increased. Moisture was likely the limiting factor as poplar shoot growth on the lightly burned-low moisture treatments was greatest under ambient conditions.

Any stress can shift the competitive balance among species within a community. The degree of change occurring depends on the response time of each species to the stress (Prentice 1986). Since individual species experience a range of conditions during their lifetimes, many species will be able to cope with some level of stress by physiologically adapting to the new conditions (see Bradshaw and McNeilly 1991). Other species may be forced out of their original habitat by species better able to take advantage of the new

conditions.

The success of all species in germinating on the heavily burned treatments in this experiment suggests a severe fire in the forest-tundra may be instrumental in the initial expansion of treeline tree species northward into the present tundra, provided viable seeds are available.

Species with short generation times and good seed dispersal patterns will most successfully expand into new areas. Paper birch and balsam poplar germinate most successfully on recently disturbed mineral soil sites. Both species' methods of seed dispersal favour long distance transport of propagules; birch seeds are effectively disseminated by wind over the snow pack. Balsam poplar seeds are also wind dispersed and can travel great distances along water channels.

Landhäusser and Wein (1993) considered the deep burning fire that occurred close to Inuvik in 1968 to be a partial analogue for the types of fires expected under future climate change scenarios. They found the post-burn density of black spruce 22 years after the fire to be much lower than pre-burn densities. For paper birch and balsam poplar, densities were higher 22 years after the fire. In addition, birch and poplar seedlings had expanded into previously treeless areas.

A severe fire in the forest-tundra in addition to changed climatic conditions may amplify the trends observed by Landhäusser and Wein (1993). In particular, paper birch may respond positively to an increase in temperature.

As treeline moves north after deep burning fires, I hypothesize that deciduous tree species, such as paper birch and balsam poplar, will take advantage of all suitable germination microsites and vigorously compete with black spruce in the early successional sequence at treeline.

Future research approaches

There are few experimental studies documenting the reproductive processes of trees growing in the northern boreal forest. In particular, there is little information for black spruce, white spruce, tamarack, paper birch, balsam poplar or trembling aspen on seed production, dispersal and optimal seedling germination and growth conditions north of the boreal region. In light of the many changes predicted for northern forests, this type of data would assist managers in making land-use decisions.

Table 1: Precipitation treatments (mm/day) applied on alternate days for each month.

MONTH	PRECIPITATION TREATMENT (mm/day) low (-50%)	average	high (+50%)
June	0.89	1.78	2.67
July	1.33	2.22	3.56
August	1.33	2.67	4.00

Table 2: Average soil temperature at three depths (n=5) for three levels of fire severity on the five warmest measurement days between 29 June and 5 August, 1992.

BURN SEVERITY	SOIL SURFACE	5CM DEPTH	15CM DEPTH
Light	33.3±1	22.7±1	6.8±0
Moderate	31.8±1	22.7±1	6.6±0
Heavy	24.4±1	16.6±0	5.5±0

Table 3: Active layer depth on different levels of fire severity, moisture and temperature (mean ± standard error).

TREATMENT	ACTIVE LAYER (cm)
Fire severity (n=18)	
light	43±2
moderate	43±2
heavy	55±2
Moisture (n=18)	
low	45±3
normal	48±2
high	47±2
Temperature (n=27)	
ambient	46±1
high	47±2

Table 4: Second year balsam poplar shoot growth (cm) (mean and standard error) under treatments of fire severity, moisture and temperature.

	FIRE SEVERITY		
	LIGHT	MODERATE	HEAVY
LOW MOISTURE with			
AMBIENT TEMPERATURE	1.9±0.6	0.7±0.2	1.1±0.3
HIGH TEMPERATURE	0.9±0.5	0.8±0.2	1.5±0.3
NORMAL MOISTURE with			
AMBIENT TEMPERATURE	0.6±0.3	1.3±0.5	0.9±0.3
HIGH TEMPERATURE	1.2±0.4	0.7±0.2	0.8±0.2
HIGH MOISTURE with			
AMBIENT TEMPERATURE	0.9±0.4	0.8±0.1	1.6±0.4
HIGH TEMPERATURE	2.3±0.3	1.0±0.3	1.3±0.3

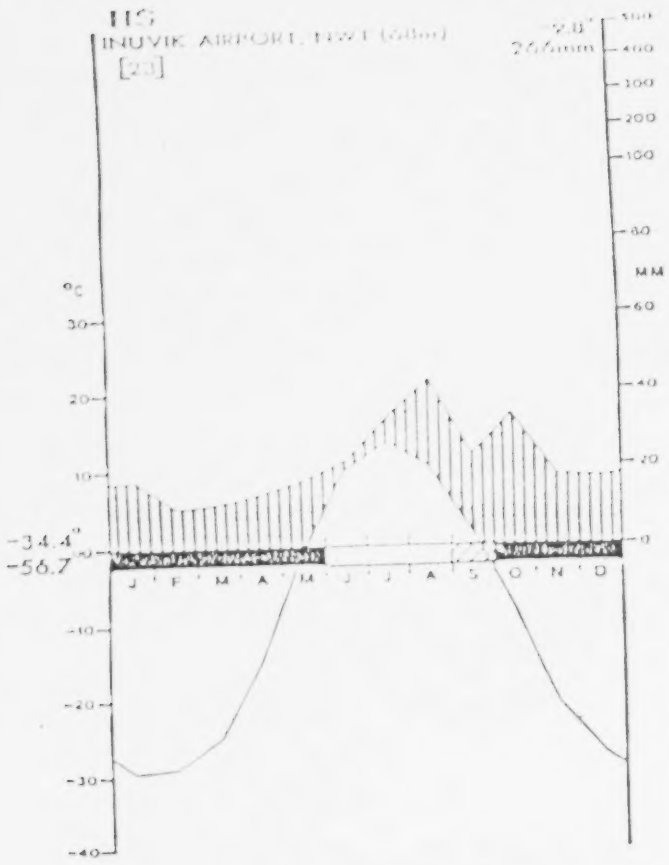

Figure 1: Climate diagram of the High Subarctic Ecoclimatic Region (data from the Inuvik Airport weather station, 1951-1981). (Adapted from Ecoregions Working Group 1989. Copyright Minister of Supply and Services Canada).

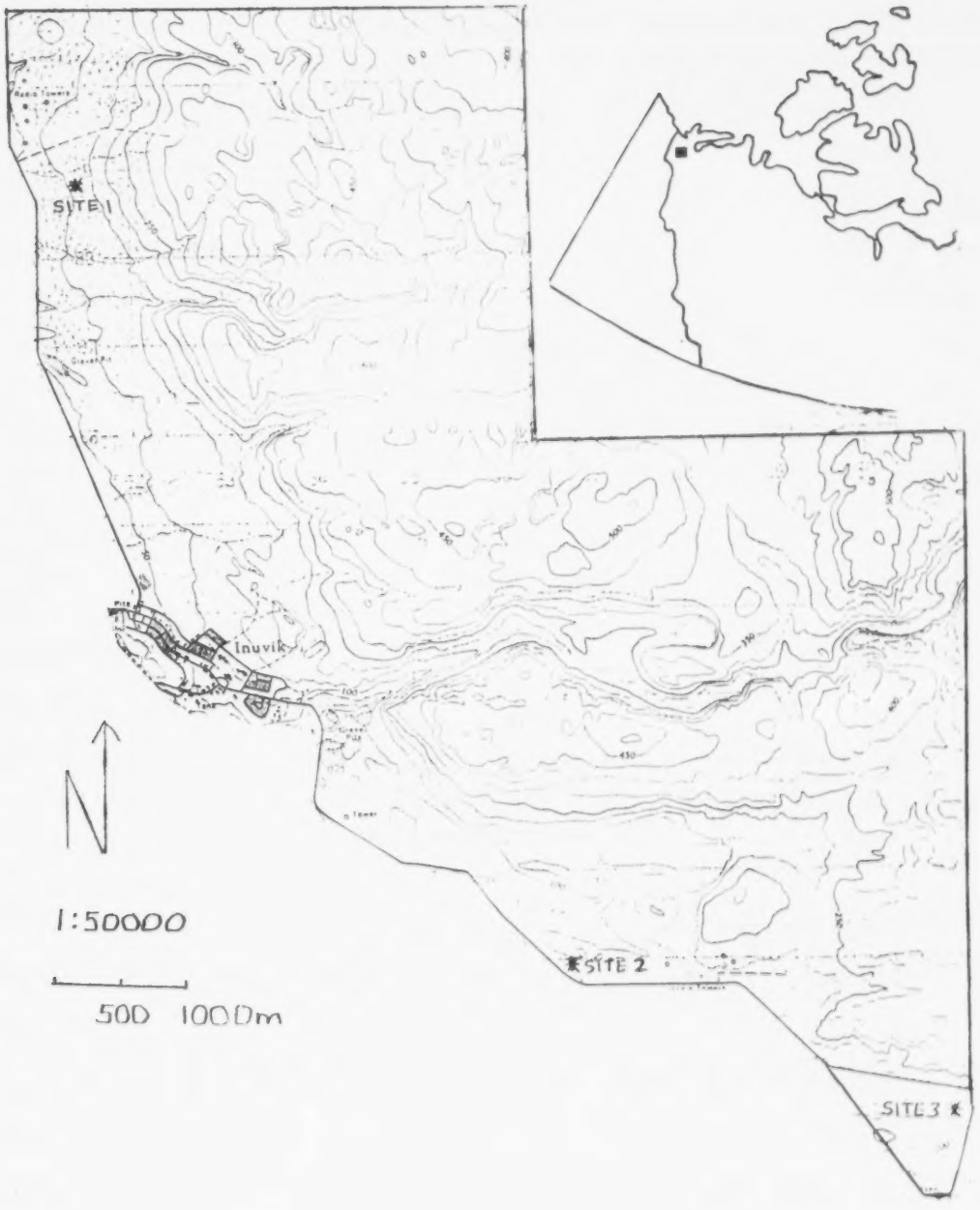

Figure 2: Location of study sites within the forest-tundra near Inuvik, NT.

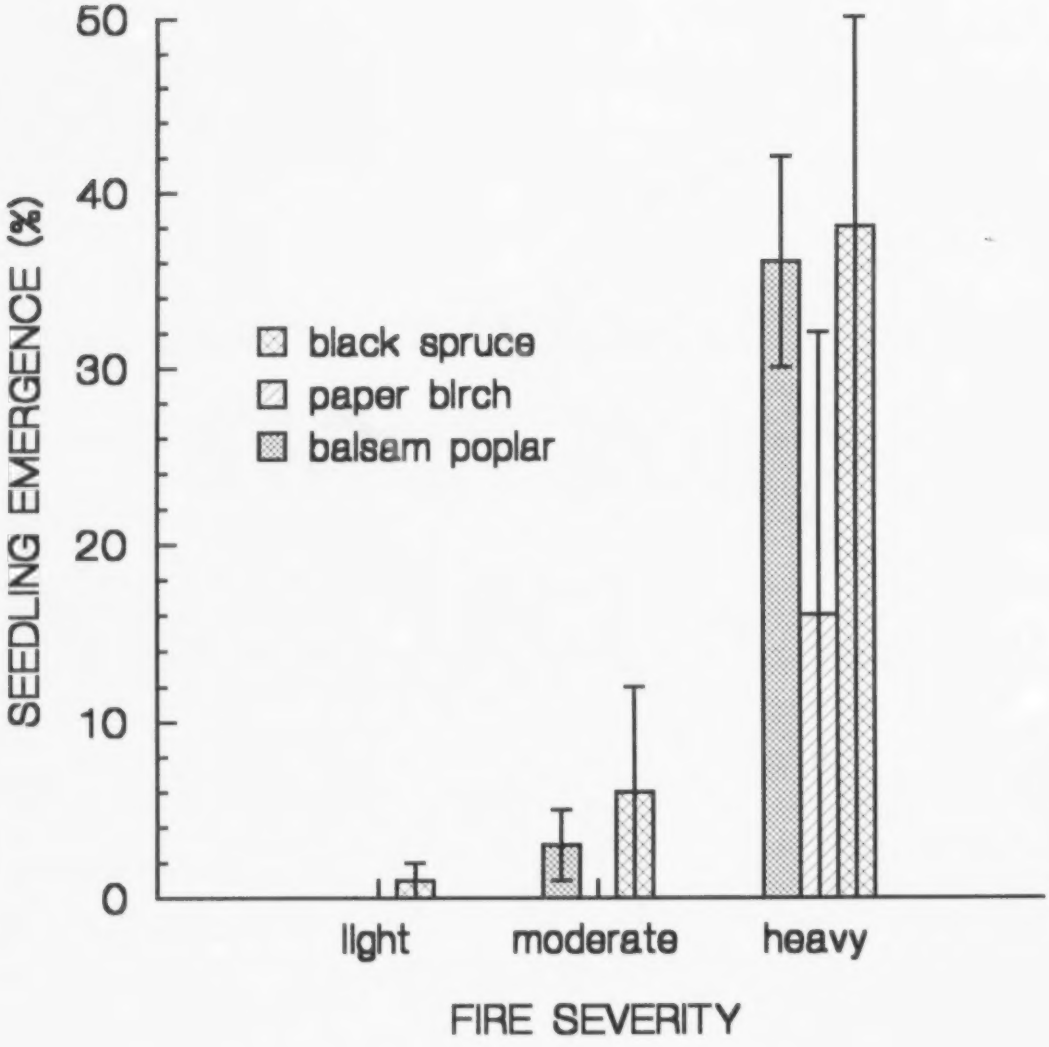

Figure 3: Percent total emergence (± standard error) of three tree species sown on three levels of fire severity treatment plots.

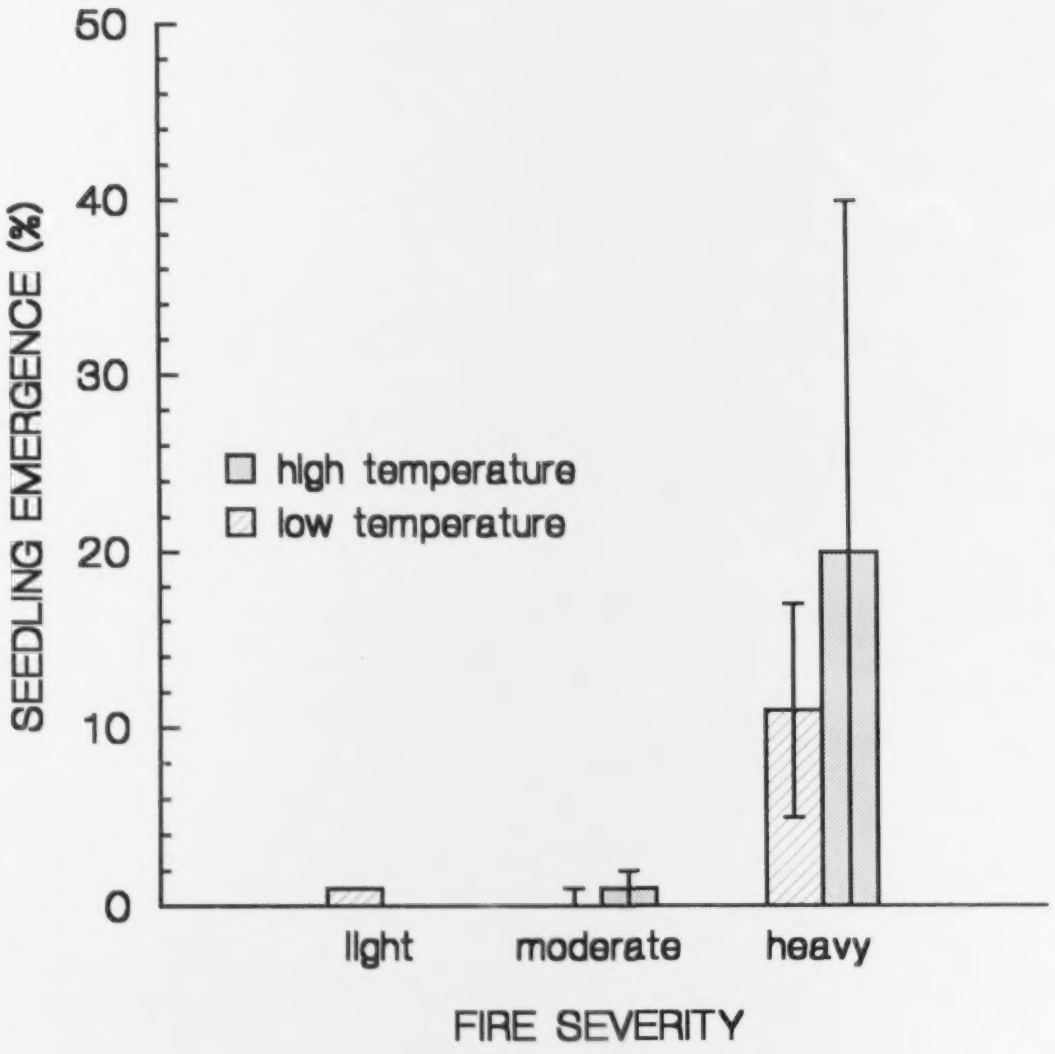

Figure 4: Percent total emergence of paper birch at three levels of fire severity treatments and two levels of temperature treatments.

LITERATURE CITED

Black, R.A. and L.C. Bliss. 1978. Recovery sequence of *Picea mariana* - *Vaccinium uliginosum* forests after burning near Inuvik, Northwest Territories, Canada. Canadian Journal of Botany 56:2020-2030.

Black, R.A. and L.C. Bliss. 1980. Reproductive ecology of *Picea mariana* (Mill.) BSP., at treeline near Inuvik, Northwest Territories, Canada. Ecological Monographs 50:331-354.

Bolin, B., B.R. Doos, J. Jager and R.A. Warrick (eds). 1986. The greenhouse effect, climate change and ecosystems. S.C.O.P.E. 29, John Wiley & Sons.

Bonan, G.B. and H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Annual Review of Ecology and Systematics 20:1-28.

Bonan, G.B. H.H. Shugart and D.L. Urban. 1990. The sensitivity of some high-latitude boreal forests to climatic parameters. Climatic Change 16:9-29.

Bradshaw, A.D. and T. NcNeilly. 1991. Evolutionary response to global climatic change. Annals of Botany 67:5-14.

Brinkman, K.A. 1974. *Betula* L. Birch. In: Schopmeyer, C.S., technical editor. Seeds of Woody Plants in the United States. Washington: U.S. Department of Agriculture, Forest Service. 252-257.

Brubaker, L.B. 1986. Responses of tree populations to climatic change. Vegetatio 67:119-130.

Burns, B.M. 1973. The climate of the Mackenzie Valley-Beaufort Sea. Volume 1. Climatological Studies Number 24. Environment Canada, Atmospheric Environment, Toronto. 227 p.

Cwynar, L.C. and J.W. Spear. 1991. Reversion of forest to tundra in the central Yukon. Ecology 72:202-212.

Day, J.H. and H.M. Rice. 1964. The characteristics of some permafrost soils in the Mackenzie Delta, N.W.T. Arctic 17:223-236.

Dyrness, C.T., and R.A. Norum. 1983. The effects of experimental fires on black spruce forest floors in interior Alaska. Canadian Journal of Forest Research 13:879-893.

Ecoregions Working Group. 1989. Ecoclimatic regions of Canada, first approximation. Ecoregions Working Group of the Canada Committee on Ecological Land Classification. Ecological Land Classification Series No. 23, Sustainable Development Branch, Canadian Wildlife Service, Conservation and Protection, Environment Canada, Ottawa, Ontario. 119 pp. and map at 1:7500000.

Elliott-Fisk, D.L. 1983. The stability of the northern Canadian tree limit. Annals of the Association of American Geographers 73:560-576.

Flannigan, M.D. and C.E. Van Wagner. 1991. Climate change and wildfire in Canada. Canadian Journal of Forest Research 21:66-72.

Foster, D.R. 1985. Vegetation development following fire in *Picea mariana* (black spruce) - *Pleurozium* forests of southeastern Labrador, Canada. Journal of Ecology 73: 517-534.

Haag, R.W. and L.C. Bliss. 1974. Energy budget changes following surface disturbances to upland tundra. Journal of Applied Ecology 11:355-374.

Henderson-Sellers, A. 1990. Modelling amd monitoring 'greenhouse' warming. Tree 5:270-275.

Koster, E.A. 1991. Assessment of climate change impacts in high-latitudinal regions. Terra 103:3-13.

Landhäusser, S.-M. and R.W. Wein. 1993. Post-fire recovery and tree establishment at the arctic treeline: climate change-vegetation response hypotheses. Journal of Ecology (in press).

Lange, P. 1993. Fire and climate change on the instability and revegetation of permafrost soils. Diplomarbeit, der Fakultat fur Biologie der Universitat Tubingen, Germany. 47 pp.

Mackay, J.R. 1978. Quaternary and permafrost features, Mackenzie Delta area. In Young, F.G., ed. Geological and geographical guide to the Mackenzie Delta area. Calgary: Canadian Society of Petroleum Geologists. 159 pp.

Maxwell, J.B. and L.A. Barrie. 1991. Atmospheric and climatic change in the Arctic and Antarctic. Ambio 18: 42-49.

Mitchell, J.F.B. and D.A. Warrilow. 1987. Summer dryness in northern mid-latitudes due to increased CO_2. Nature 330:238-240.

Morneau, C. and S. Payette. 1989. Post-fire lichen-spruce woodland recovery at the limit of the boreal forest in northern Quebec. Canadian Journal of Botany 67:2770-2787.

Overpeck, J.T., D. Rind and R. Goldberg. 1990. Climate-induced changes in forest disturbance and vegetation. Nature 343:51-53.

Pettapiece, W.W. 1974. A hummocky permafrost soil from the subarctic of northwestern Canada and some influences of fire. Canadian Journal of Soil Science 54:343-355.

Prentice, I.C. 1986. Vegetation responses to past climatic variation. Vegetatio 67:131-141.

Racine, C.H., L.A. Johnson and L.A. Viereck. 1987. Patterns of vegetation recovery after tundra fires in northwestern Alaska, U.S.A. Arctic and Alpine Research 19:461-469.

Rind, R., R. Goldberg, and R. Ruddy. 1989. Change in climate variability in the 21st century. Climatic Change 14:5-37.

Rizzo, B. and E. Wiken. 1992. Assessing the sensitivity of Canada's ecosystems to climatic change. Climatic Change 21:37-55.

Roots, E.F. 1989. Climate change: high latitude regions. Climatic Change 15:223-253.

Rowe, J.S. 1972. Forest regions of Canada. Canadian Forest Service Publication No. 1300. Reprint 1977. 172 pp.

Safford, L.O. 1974. *Picea* A. Dietr. Spruce. In: Schopmeyer, C.S., technical editor. Seeds of Woody Plants in the United States. Washington: U.S. Department of Agriculture, Forest Service. 587-597.

Schreiner, E.J. 1974. *Populus* L. Poplar. In: Schopmeyer, C.S., technical editor. Seeds of Woody Plants in the United States. Washington: Department of Agriculture, Forest Service. 645-655.

Sirois, L. and S. Payette. 1991. Reduced postfire regeneration along a boreal forest-forest-tundra transect in northern Quebec. Ecology 72:619-627.

Thomas, P.A. and R.W. Wein. 1985. The influence of shelter and the hypothetical effect of fire severity on the postfire establishment of conifers from seed. Canadian Journal of Forest Research 15:148-155.

Timoney, K.P. and R.W. Wein. 1991. The areal pattern of burned tree vegetation in the subarctic region of northwestern Canada. Arctic 44:223-230.

Tryon, P.R. and F.S. Chapin III. 1983. Temperature control over root growth and root biomass in taiga forest trees. Canadian Journal of Forest Research 13:827-833.

Van Cleve, K., L. Oliver, R. Schlentner, L.A. Viereck and C.T. Dyrness. 1982. Productivity and nutrient cycling in the taiga forest ecosystems. Canadian Journal of Forest Research 13:747-766.

Viereck, L.A. 1979. Characteristics of treeline plant communities in Alaska. Holarctic Ecology 2:228-238.

Viereck, L.A. and M.J. Foote. 1970. The status of *Populus balsamifera* and *P. trichocarpa* in Alaska. Canadian Field Naturalist 84:169-173.

Viereck, L.A. and L.A. Schandelmeier. 1980. Effects of fire in Alaska and adjacent Canada: a literature review. BLM-Alaska Technical Report 6. U.S. Department of the Interior, Bureau of Land Management.

Viereck, L.A. and K. Van Cleve. 1984. Some aspects of vegetation and temperature relationships in the Alaskan taiga. In McBeath, J.H., ed. The potential effects of carbon dioxide induced climatic changes in Alaska. Proceedings of a conference, University of Alaska-Fairbanks, Misc. publication 83-1. 129-143.

Viereck, L.A., J. Foote, C.T. Dyrness, K. Van Cleve, D. Kane and R. Seivert. 1979. Preliminary results of experimental fires in the black spruce type of interior Alaska. U.S. Forest Service Pacific Northwest Forest and Range Experiment Station Research Note PNW-332. 37p.

Weber, M.G. 1975. Nutrient redistribution following fire in tundra and forest-tundra. M.Sc. thesis, University of New Brunswick, Fredericton. 69 pp.

Wein, R.W. 1975. Vegetation recovery in the arctic-tundra and tundra after fire. A.L.U.R. 74-75-62. Ottawa: Department of Indian Affairs and Northern Development. 81 pp.

Wein, R.W. and D.A. MacLean. 1983. The role of fire in northern circumpolar ecosystems. SCOPE 18. Toronto: John Wiley & Sons. 322 pp.

Woodley, S.J. 1979. Nutrient loss from burned arctic plant communities. M.Sc. thesis. University of New Brunswick, Fredericton. 51 pp.

Zasada, J.C., T.L. Sharik and M. Nygren. 1991. The reproductive process in boreal forest trees. In Shugart, H.H, Leeman, and Bonan, G.B., eds. Systems analysis of the global boreal forest. London: Cambridge University Press. 85-125.

Zasada, J.C., R.A. Norum, C.E. Teutsch and R. Densmore. 1987. Survival and growth of planted black spruce, alder, aspen and willow after fire on black spruce/feather moss sites in interior Alaska. The Forestry Chronicle 63:84-88.

Zasada, J.C. R.A. Norum, R.M. Van Veldhuizen and C.E. Teutsch. 1983. Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce/feathermoss stands in Alaska. Canadian Journal of Forest Research 13:903-913.

APPENDIX 1

Statistical model for three-way Analysis of Variance (with pooled block interactions) for emergence, winter survival and early seedling growth experiments.

SOURCE OF VARIATION	DEGREES OF FREEDOM
fire severity (f) = j	2
moisture (m) = k	2
temperature (t) = l	1
f x m	4
f x t	2
m x t	2
f x m x t	4
error (e) = m	36
total	53

model: $Y = mean + f_j + m_k + t_l + f_m + fm_{jk} + ft_{jl} + mt_{kl} + fmt_{jkl} + e_{m(ijkl)}$

APPENDIX 2

Effects of fire severity, moisture and temperature on active layer depth (using Analysis of Variance with pooled block interactions).

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire	2	7.32	0.000
Moisture	2	0.94	0.105
Temperature	1	0.41	0.987
Error	32	75.44	0.087

n=52, α=0.05

APPENDIX 3

Effects of fire severity, moisture and temperature on the emergence of a) black spruce, b) paper birch and c) balsam poplar seeds (using Analysis of Variance with pooled block interactions).

a) Black spruce (emergence)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire	2	7209.834	0.000
Moisture	2	3.352	0.983
Temperature	1	507.018	0.114
Error	32	192.290	

n=52, α=0.05

b) Paper birch (emergence)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P- VALUE
Fire (F)	2	1778.417	0.000
Moisture	2	36.725	0.576
Temperature (T)	1	230.004	0.070
F x T	2	209.204	0.054
Error	32	65.374	

n=52, α=0.05

c) Balsam poplar (emergence)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire	2	6604.139	0.000
Moisture	2	110.674	0.621
Temperature	1	282.965	0.274
Error	32	228.731	

n=52, α=0.05

APPENDIX 4

Effects of fire severity, moisture and temperature on first-year shoot growth of a) black spruce b) paper birch and c) balsam poplar seedlings (using Analysis of Variance with pooled block interactions).

a) Black spruce (first-year shoot growth)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire	2	2.859	0.312
Moisture	2	4.333	0.181
Temperature	1	8.608	0.069
Error	17	2.292	

n=25, α=0.05

b) Paper birch (first-year shoot growth)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire	2	0.405	0.731
Moisture	2	0.501	0.680
Temperature	1	1.799	0.253
Error	14	1.263	

n=22, α=0.05

c) Balsam poplar (first-year shoot growth)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire	2	0.768	0.335
Moisture	2	1.662	0.111
Temperature	1	1.017	0.231
Error	16	0.656	

n=32, α=0.05

APPENDIX 5

Effects of fire severity, moisture and temperature on the winter survival of a) black spruce b) paper birch and c) balsam poplar seedlings (using Analysis of Variance with pooled block interactions).

a) Black spruce (winter survival)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire	2	4671.838	0.031
Moisture	2	2440.009	0.135
Temperature	1	1573.625	0.242
Error	15	1061.335	

n=23, α=0.05

b) Paper birch (winter survival)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire	2	1144.593	0.499
Moisture	2	1266.180	0.466
Temperature	1	2251.964	0.252
Error	12	1552.82	

n=20, α=0.05

c) Balsam poplar (winter survival)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire	2	3201.940	0.065
Moisture	2	207.755	0.808
Temperature	1	735.004	0.396
Error	14	958.429	

n=30, α=0.05

APPENDIX 6

Effects of fire severity, moisture and temperature on second-year shoot growth of a) black spruce b) paper birch and c) balsam poplar seedlings (using Analysis of Variance with pooled block interactions).

a) Black spruce (second-year shoot growth)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire (F)	2	0.236	0.424
Moisture (M)	2	0.339	0.296
Temperature (T)	1	0.759	0.102
FxMxT	4	0.659	0.064
Error	34	0.268	

n=54, α=0.05

b) Paper birch (second-year shoot growth)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire (F)	2	0.377	0.600
Moisture (M)	2	1.391	0.163
Temperature (T)	1	1.307	0.189
FxMxT	4	0.572	0.542
Error	34	0.727	

n=54, α=0.05

c) Balsam poplar (second-year shoot growth)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire (F)	2	0.493	0.178
Moisture (M)	2	0.299	0.344
Temperature (T)	1	0.012	0.836
F x M x T	4	0.906	0.021
Error	33	0.271	

n=53, α=0.05

APPENDIX 7

Effects of fire severity, moisture and temperature on leaf area of a) paper birch and b) balsam poplar seedlings (using Analysis of Covariance with pooled block interactions for paper birch and Analysis of Variance with pooled block interactions for balsam poplar).

a) Paper birch (leaf area)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire (F)	2	5770.566	0.028
Moisture (M)	2	1185.935	0.449
Temperature (T)	1	2181.754	0.228
FxMxT	4	1343.597	0.459
covariate*	1	38902.582	0.000
Error	34	1445.510	

n=54, α=0.05
* covariate=initial seedling height

b) Balsam poplar (leaf area)

SOURCE OF VARIATION	DEGREES OF FREEDOM	MS	P-VALUE
Fire (F)	2	317.281	0.476
Moisture (M)	2	195.505	0.630
Temperature (T)	1	287.604	0.412
FxMxT	4	69.710	0.954
Error	33	417.360	

n=53, α=0.05